

TEMPORAL PATTERNS OF HYPERPARASITOID EMERGENCE FROM *COTESIA MELANOSCELUS* (HYMENOPTERA: BRACONIDAE) COCOONS¹

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ABSTRACT: *Cotesia melanoscelus* is an important parasitoid of the gypsy moth whose effectiveness is reduced by a complex of hyperparasitoids. The hyperparasitoid complex of *C. melanoscelus* is characterized in the three different geographic provinces of Maryland, and the pattern of progeny adult emergence from parasitized *C. melanoscelus* cocoons as a function of month of attack is compared for the more prominent hyperparasitoid species. Several strategies for apportioning progeny adult emergence to meet the challenges and opportunities of within-season (horizontal) and overwinter (vertical) propagation were found and elucidated. The simplest strategy was that of *Ooencyrtus kuvanae*, a species that produced new broods all year long without any obvious need for diapause. A more typical strategy used by several species was to produce a series of new broods until late summer, and then to produce a brood that undergoes diapause with adult emergence in the spring. A more complex strategy was used by *Gelis tenellus*, which, beginning in late spring, partitioned its progeny so that some progeny emerged as an immediate summer generation, while others from the same attack cohort entered diapause and emerged in the spring. The most complex strategy was that used by *G. apantelis* and *G. obscurus*. Beginning in late spring, the progeny from these two species were partitioned so that some progeny would emerge as adults for an immediate summer generation and others from the same attack cohort would emerge in September to bolster the adult population that then produced the diapausing generation. This pattern persisted as the summer progressed, leading to a continuous emergence of multiple generations while simultaneously building up a fall generation upon which the overwintering survival of the species largely depends.

Cotesia melanoscelus (Ratzeburg) is an abundant parasitoid of early stages (instars 1-3) of the gypsy moth, *Lymantria dispar* (L.) (Lepidoptera: Lymantriidae) in North America. *C. melanoscelus* has been reared exclusively from three species of field-collected lymantriids: the gypsy moth, the satin moth, *Leucoma salicis* (L.), and the white-marked tussock moth *Hemerocampa leucostigma* (J. E. Smith). Invertebrate predators and a complex of hyperparasitoids seriously reduce the effectiveness of this parasitoid (Wieber et al. 1995b). This complex has been characterized in New England (Muesebeck and Dohanian 1927, Proper 1934, Weseloh 1978, 1979, 1983, 1986), New York (Grimble 1976), and Ontario, Canada (Bourchier and Nealis 1992), but

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not in the more southern range of the gypsy moth. The present paper is from a large data set that characterized the hyperparasitoid complex of *C. melanoscelus* in the three different geographic provinces of Maryland: the coastal plain, the Piedmont Plateau, and the Appalachian Mountains. A previous paper from this data set examined niche partitioning (resource sharing) by several species of *Gelis* attacking supplied *C. melanoscelus* cocoons (Wieber et al. 1995a). Temporal and spatial overlap of the *Gelis* spp. allowed competition among the species for utilization of the *C. melanoscelus* resource that was mitigated in part by differing temporal patterns of attack among the species, and by differing preferences among the species for tree height. A general characterization of the hyperparasitoid complex of *C. melanoscelus* in Maryland was recently published in this journal (Wieber et al. 2001). The present paper compares the pattern of progeny (adult hyperparasitoid) emergence from parasitized *C. melanoscelus* cocoons as a function of time of attack for the more prominent hyperparasitoid species as an additional parameter that might facilitate resource partitioning.

MATERIALS AND METHODS

The materials and methods used in this study have been presented in detail elsewhere (Wieber et al., 1995a, 1995b, 1996), and a condensed version is given here with emphasis on aspects of the study pertinent to the data now presented. This paper concerns the approximately 8,000 hyperparasitoids (see Wieber et al. 2001 for details) that emerged from these cocoons. There were three study sites. The coastal plain site in southern Maryland was midway between Poplar Hill and Aquasco, in the Patuxent River Park, at 38° 36' 45" latitude, 76° 43' longitude (Benedict Quadrangle, U. S. Geological Survey 7.5 Minute Series Topographic Map). This was along a power line parallel to Aquasco Farm Road, at 20-50 m altitude. The Piedmont Plateau (north-central Maryland) site was located along the north bank of Prettyboy Reservoir at 39° 37' 15" latitude, 76° 45' longitude (Hereford Quadrangle, U. S. Geological Survey 7.5 Minute Series Topographic Map), at 200-240 m altitude. The Appalachian Mountains (western Maryland) site was located northwest of Barton, MD, along Swamp Road in the Savage River State Forest, at 39° 35' latitude, 79° 3' 15" longitude (Barton Quadrangle, U. S. Geological Survey 7.5 Minute Series Topographic Map), at 730-800 m altitude. Cocoons of *C. melanoscelus* were placed in the field at periodic intervals from March 1986 through March 1987. There were 20 exposure periods each at the coastal plain (new cohorts placed out on Julian dates 64, 85, 106, 134, 148, 168, 176, 190, 204, 219, 231, 248, 267, 289, 310, 330, and 351 in 1986, and 007, 035, 058, ending on 076 in 1987) and Piedmont Plateau sites (new cohorts placed out on Julian dates 63, 85, 108, 128, 148, 163, 176, 191, 205, 219, 233, 246, 267, 288, 310, 329, and 351 in 1986, and 008, 037, 057, and ending on 077 in 1987) and 17 exposure periods at the western Maryland site (new cohorts placed out on Julian dates

69, 88, 115, 150, 163, 178, 193, 205, 221, 247, 269, 290, 312, 338 in 1986, and 010, 037, 063, ending on 077 in 1987). The strain of *C. melanoscelus* used for all exposure periods was from a laboratory colony of the established North American parasitoid that was descended from material collected from Egg Hill, Maryland (in Cecil County) by K. W. Thorpe in 1984. However, at each site, 5 consecutive exposure periods (25 June through 5 September 1986) were used to compare the susceptibility to the overall hyperparasitoid communities of the Maryland strain with that of a Korean strain. Results, presented in Wieber et al. (1996), demonstrated that there was little or no difference in measurements of the hyperparasitoid communities attacking the Maryland and the Korean strains; therefore, data for the two strains are combined in the present report. Both strains of parasitoid were reared by the procedure of Kolodny-Hirsch (1988), with photophase kept less than 16 h to yield cocoons containing diapausing third-instar larvae. Cocoons were attached to 10-cm diameter white cardboard tab ice cream cup lids using polyvinyl glue. Five cocoons (termed "hidden") were glued to a lid and then a second lid was stapled to the first lid over the top of the cocoons, allowing a 1-cm gap for hyperparasitoid entry. Five additional cocoons (termed "exposed") were placed in a line on a second lid without a cover, which was placed on the opposite side of the cage from the "hidden" cocoons. Once in the field, the lids bearing the cocoons were placed in 10-cm X 10-cm X 10-cm cages constructed of 5-mm mesh wire screening to protect against vertebrate predators but allowing free access for the hyperparasitoids. The caged cocoons were placed at ground level and at 1.5 m on 40 trees at each site, and at an average of 7-m in the canopy of 5 of those trees. However, since the focus of this paper is strictly on the emergence patterns of the hyperparasitoids, factors such as hidden versus exposed and height on the tree are pooled for each exposure period. Cocoons were exposed for 2-3 week periods, and were then replaced by a new cohort of cocoons. The retrieved cocoons were returned to Beltsville, Maryland and individual cocoons placed in 30-ml sealed, plastic cups where they were held under ambient conditions in a field insectary and monitored periodically for emergence of *C. melanoscelus* or hyperparasitoids. Observations of emergence were made once or twice a week from 25 April 1986 until 31 December 1986 and once or twice a month from 1 January 1987 until 17 March 1988.

Chi-square tests of the association between species and period of emergence were performed separately for each period of attack (SAS 1989; PROC FREQ). For the purpose of this analysis attacks that occurred in April, May, and June were combined into a single category to reduce the number of zero values.

Identifications: Specimens of all hyperparasitoid species were sent to appropriate authorities for identification. Ichneumonidae (*Gelis tenellus* (Say), *G. apantelis* (Cushman), *G. obscurus* (Cresson), *G. species-4* (undescribed), *Lyneon orbis* (Say), *Isdromas lycaenae* (Howard), *Lysibia mandibularis*

(Prov.) and *Acrolyta* sp.) were determined by R. W. Carlson, Systematic Entomology Laboratory (SEL), ARS-USDA, Beltsville, MD. Encyrtidae, including *Ooencyrtus kuvanae* (Howard), *Ooencyrtus* species-2, and *Cheiloneurus* sp., were determined by M. E. Schauff, SEL, who also identified *Anastatus pearsalli* Ashmead (Eupelmidae), and *Aprostocetus* sp. (Eulophidae). *Aprostocetus* specimens were identified using the concept of the genus contained in LaSalle (1994). E. E. Grissell, SEL, identified the *Ceratosmicra meteori* Burks (Chalcididae), *Eurytoma verticillata* (F.) (Eurytomidae), and the Pteromalidae (*Dibrachys cavus* (Walker), *Tritneptis scutellata* (Muesebeck), and *Hypopteromalus inimicus* Muesebeck). G. Gibson, Biosystematics Research Centre, Ottawa, Ontario, Canada, confirmed the *A. pearsalli* identification and identified the *Arachnophaga picea* (Riley) (Eupelmidae) and a second, undescribed, *Anastatus* species, *Anastatus* n. sp. near *reduvii*. Although most of the *Anastatus* specimens keyed to *A. pearsalli*, there is no key for the males of this group, so for this paper, all *Anastatus* material is combined as *Anastatus* species complex.

RESULTS AND DISCUSSION

Twenty species of hyperparasitoids were identified emerging from *C. melanoscelus* cocoons from one or more of the Maryland locations. Several of these species can act facultatively or preferentially as tertiary parasitoids (Muesebeck and Dohanian 1927). Our results demonstrated high levels of parasitism for *C. melanoscelus* cocoons at all 3 Maryland locations. This aspect of the study was presented in Wieber et al., 1995b, and will not be discussed in detail here. A detailed accounting of the fate of the approximately 48,000 exposed *C. melanoscelus* cocoons is given in Wieber et al. 1995b). Of these exposed cocoons, numbers yielding hyperparasitoid adults (from the 3 locations combined) were as follows. For the Superfamily Ichneumonoidea, family Ichneumonidae: *Gelis apantelis* - 2266, *G. obscurus* - 1655, *G. tenellus* - 1310, *G. sp. # 4* - 156, *Lyneon orbis* - 3, *Isdromas lycaenae* - 16, *Lysibia mandibularis* - 4, *Acrolyta* sp. - 33. Additionally, *C. melanoscelus* cocoons yielded recoveries of hyperparasitoids from 6 families in the Superfamily Chalcidoidea. These included (Family Pteromalidae) *Dibrachys cavus* - 321, *Tritneptis scutellata* - 26, *Hypopteromalus inimicus* - 260; (Family Encyrtidae) *Ooencyrtus kuvanae* - 477, *Ooencyrtus* sp # 2 - 7, *Cheiloneurus* sp. - 2; (Family Eupelmidae) *Anastatus* mixed spp. - 1349, *Arachnophaga picea* - 117; (Family Eulophidae) *Aprostocetus* sp. - 20; (Family Chalcididae) *Ceratosmicra meteori* - 46; (Family Eurytomidae) *Eurytoma verticillata* - 119. This aspect of the data set will be discussed in a separate paper.

Adult emergence of the *Gelis* complex. In Maryland, the *Gelis* complex (*G. apantelis*, *G. obscurus*, *G. tenellus* and *Gelis* species # 4) accounted for 65.6% of the parasitized *C. melanoscelus* cocoons. How do these closely related species manage to share the available prey so that one species does not

Table 1. Comparison of the emergence patterns of 3 species of hyperparasitoids of the *Gelis* complex from *Cotesia melanoscelus* cocoons attacked during the indicated period. Combined results for three Maryland locations for cohorts of cocoons exposed at two-three week intervals from March 1986 to March 1987.

Period of Attack	# Cocoons Attacked	Period of hyperparasitoid adult progeny emergence						Spring '87 (diapause)	
		May	June	July	Aug.	Sept.	Oct.	Nov.-Jan.	
<i>Gelis apantelis</i>									
Mar-May	211	10	134	6	0	54	4	3	0
Early June	267		107	40	1	113	5	1	0
Late June	206			77	10	95	21	2	1
Early July	428			212	13	96	102	0	5
Mid-July	323			92	129	62	36	3	1
Late July	287				220	53	10	1	3
August	223				15	114	69	2	23
September	117						32	11	74
Oct.-Dec.	218							2	216
N	2280	10	241	427	388	587	279	25	323
<i>Gelis obscurus</i>									
Mar-May	246	5	159	2	1	19	0	0	0
Early June	132		62	39	2	28	1	0	0
Late June	146			92	1	49	4	0	0
Early July	147			87	10	40	9	1	0
Mid-July	48			10	20	16	1	0	1
Late July	79				69	8	1	0	1
August	107					51	36	1	19
September	131						51	1	79
Oct.-Dec.	609							6	603
N	1645	65	221	230	103	211	103	9	703
<i>Gelis tenellus</i>									
Mar-May	97	5	89	2	1	0	0	0	0
Early June	39		33	3	0	1	0	0	2
Late June	67			56	1	1	0	0	9
Early July	198			157	5	5	1	1	29
Mid-July	180			9	119	8	3	1	40
Late July	154					104	10	0	39
August	72						27	12	33
September	124							15	103
Oct.-Dec.	386							2	386
N	1317	5	122	227	230	52	32	10	639

dominate the others? A previous paper from this data set (Wieber et al. 1995a) examined niche partitioning by the 4 *Gelis* species in utilizing the provided *C. melanoscelus* cocoons. Data were presented on the periodicity of attack, the effect of tree species, and the effects of exposure height, for these 4 species. Differences were found in height preference and timing of attack, demonstrating some aspects of resource partitioning. The present paper focuses on an additional biological parameter that may influence resource partitioning; that is, the periodicity of emergence of adult hyperparasitoids from *C. melanoscelus* cocoons as a function of month of attack. A staggered emergence of progeny from cocoons attacked during the same exposure period was recorded for the 3 principal species that varied from species to species, and within a species, from month to month (Table 1). For instance, of the 211 *C. melanoscelus* cocoons attacked in March through May by *G. apantelis*, 10 adults emerged in May, 134 adults emerged in June, 6 adults emerged in July, 54 adults emerged in September, and 7 adults emerged from October through January. Thus the progeny were partitioned so that some progeny would emerge as an immediate summer generation, while others would emerge in September to bolster the adult population that produces the diapausing generation. This pattern persisted as the summer progressed, leading to multiple generations while simultaneously building up a fall generation upon which the overwintering survival of the species largely depends. Most of the individuals that actually underwent diapause emerged from cocoons attacked in September or later. *G. obscurus* exhibited a similar emergence pattern (Table 1). However, *G. tenellus* has evolved a related but different solution to the problem of overwintering. Beginning with the June attacks, the progeny of *G. tenellus* were partitioned so that some progeny would emerge as an immediate summer generation, while others would enter diapause and emerge the following spring. There was no bolstering of the autumn generation such as was seen for *G. apantelis* and *G. obscurus*. Analysis of the present study demonstrated that the 3 major species of *Gelis* vary in the partitioning of emergence of their progeny (Table 2). For instance, adults would emerge from some cocoons parasitized in June by *G. apantelis* within 50 days, which we termed "summer emergence," while other adults would emerge from the same set of cocoons in 50 to 120 days or longer, but did not overwinter. We termed this "autumn emergence." Adult hyperparasitoids that overwintered in the host cocoon and emerged during the subsequent spring, called the "spring generation," were considered to have been in diapause. Grouping the data together by time periods allowed statistical examination of the emergence patterns of these species by chi square analysis (Table 2). The patterns of emergence among the species were significantly different at $P < 0.0001$ for attacks occurring in April-June, July, August, and September, but not for the October-January period. The different emergence patterns are examined in Figure 1 as percentages of each species emerging in the summer, the autumn, or the following spring, for five periods of attack. *G.*

Table 2. Comparison of the emergence patterns of 3 species of hyperparasitoids of the *Gelis* complex from *Cotesia melanoscelus* cocoons, attacked during the indicated period, apportioned as direct summer emergence (within 50 days of attack), delayed emergence (over 50 days but without overwintering) or emerging in the spring after overwintering (diapause). Combined results for three Maryland locations for cohorts of cocoons exposed at two-three week intervals from March 1986 to March 1987.

Period of Attack	Period of hyperparasitoid adult progeny emergence									Signif. by chi sq. (df) ¹
	Summer emergence			Autumn emergence			Spring emergence (diapause)			
	<i>apantelis</i>	<i>obscurus</i>	<i>tenellus</i>	<i>apantelis</i>	<i>obscurus</i>	<i>tenellus</i>	<i>apantelis</i>	<i>obscurus</i>	<i>tenellus</i>	
April-June	373	419	88	310	105	4	1	0	11	229.2*(4)
July	727	205	406	302	67	18	9	2	108	336.9*(4)
August				200	88	39	23	19	33	45.3*(2)
September				43	52	21	74	79	103	17.8*(2)
Oct.-Jan.				2	6	2	216	603	384	0.66(2)

¹ Chi-square tests of the association between species and period of emergence were performed separately for each period of attack (SAS 1989; PROC FREQ). For the purpose of this analysis, attacks that occurred in April, May, and June were combined into a single category to reduce the number of zero values. Values denoted by * have differences in emergence patterns among the species significant at $P < 0.0001$.

apantelis and *G. obscurus* displayed similar patterns of emergence that can be termed a "summer-autumn" emergence strategy, with a considerable percentage of the adults from cocoons parasitized from April to July emerging within 50 days (summer emergence) to set up one or more summer generations, and a lesser percentage emerging in the late summer and fall (autumn emergence) to bolster the population whose attacks lead to the overwintering generation. Few *G. apantelis* or *G. obscurus* adults from *C. melanoscelus* cocoons attacked before late summer exhibited diapause. In contrast, *G. tenellus* partitioned progeny adult emergence quite differently. While a portion of *G. tenellus* adults from cocoons attacked in spring or early summer exhibited "summer emergence", setting up multiple generations, "autumn emergence" was greatly reduced. Instead of a portion of the *G. tenellus* adults from cocoons attacked in spring or early summer exhibited overwintering "spring emergence". This can be called a "summer-spring" strategy. *G. tenellus* clearly relied less on its fall generation to assure its overwintering, with the proportion of spring emergence (diapause) for each attack cohort increasing steadily as the season progressed. Virtually all adults of all 3 *Gelis* species that emerged from cocoons attacked after the first of October underwent diapause (Fig. 1).

Muesebeck and Dohanian (1927) reported that *G. apantelis* and *G. obscurus* (as *G. bucculatricis* (Ashmead)) (see p 408 in Krombein et al. 1979 for synonymy) developed from egg to adult in from 14 to 28 days, and had two to three generations per year. With the hibernating generation, the fully developed larvae remain in the host cocoon from August until the following spring. Muesebeck and Dohanian (1927) also reported that the total period from egg

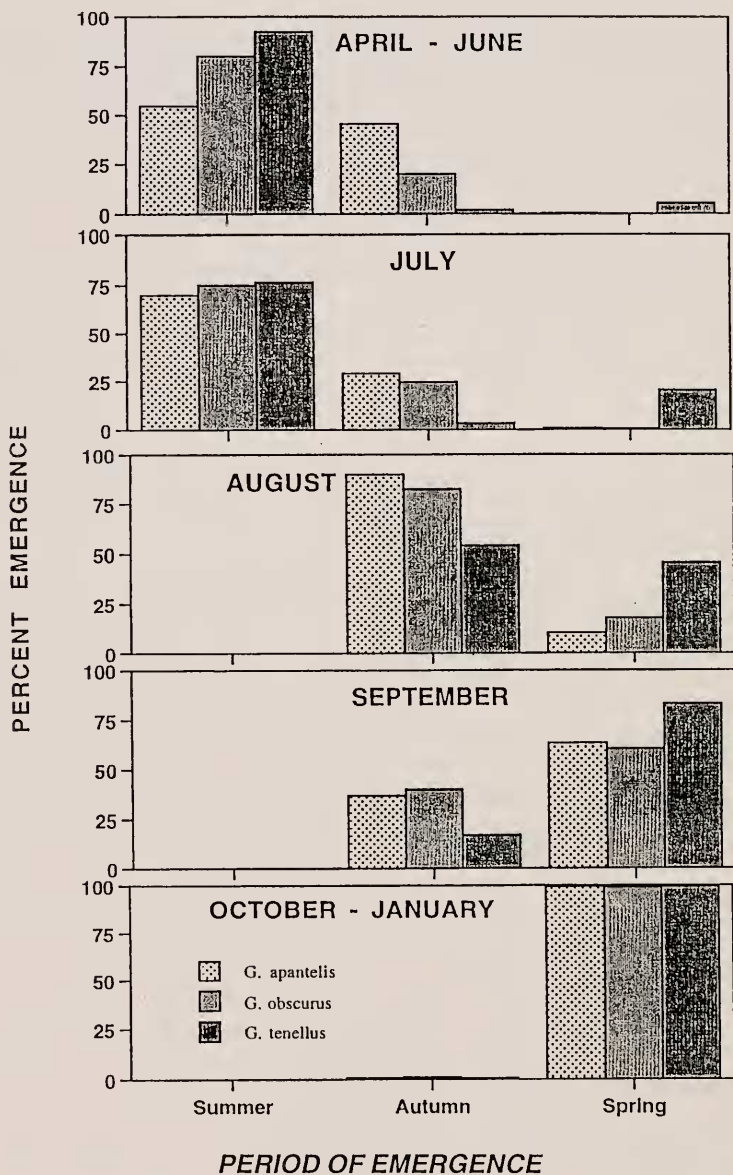


Figure 1. Percentages of 3 species of hyperparasitoids of the genus *Gelis* (*G. apantelis*, *G. obscurus*, *G. tenellus*) emerging from *C. melanoscelus* cocoons in the summer months, in the autumn months or in spring after undergoing diapause, as a function of month of attack.

to adult for the development of *G. tenellus* was 15 to 30 days, depending on temperature, and that there are up to 4 generations per year. Muesebeck and Dohanian (1927) also remarked that there were numerous cases where several cocoons were attacked by the same individual, some producing adult *G. tenellus* after 18 to 24 days to begin another generation, and others failing to yield adults until the following spring. Giron (1978) found that the mean developmental time of *G. tenellus* was 17 days at 25°C and 30% RH. Adults lived ca. 40 days with peak oviposition at days 6-10. The critical photoperiod for diapause induction was 11-14 h of daylight but diapause incidence never fell below 30%, even at 20-h photophase. All photophases under 11 h induced diapause at rates of 98-100%.

Gelis sp. #4 (undescribed) emerging from *C. melanoscelus* cocoons attacked before August did not display the delayed emergence seen for the other 3 *Gelis* sp, and generally emerged within a month or 6 weeks after attack. This implies that it has several summer generations a year. Diapause (spring emergence) was first noted for *Gelis* sp. #4 adults emerging from cocoons exposed in August (1 diapausing adult out of 20) and September (4 diapausing adults out of 7).

Four other ichneumonid hyperparasitoids (*Acrolyta* sp., *Isdromas lycaenae*, *Lysibia mandibularis*, and *Lymeon orbis*) emerged from the exposed *C. melanoscelus* cocoons, but none in numbers permitting an analysis of adult emergence.

Adult emergence of the Eupelmidae. *Anastatus* mixed species were active in the Piedmont Plateau site and the Coastal Plain site, but not the Appalachian Mountain site. *Anastatus* was active against *C. melanoscelus* from May through September, with attacks peaking in late-May to mid-June. Combining the data from the 2 sites for adult progeny emergence (Table 3), we found that 21 % of the 332 *Anastatus* adults emerging from cocoons attacked in the spring (May) emerged in the early summer (June-July), while most of the remaining emergence occurred in the late summer (Aug.-Sep.). Not one adult from this group emerged the following spring. Of the 889 *Anastatus* adults emerging from cocoons attacked in the early summer (June-July), 23% emerged in the early summer (June-July), and again most of the remaining emergence occurred in the late summer (August-September). Again, no adult from this group emerged the following spring. Of the 44 *Anastatus* adults emerging from cocoons attacked in the late summer (August), 57% emerged in the late summer (Aug.-Sep.), while 43% underwent diapause and emerged the following spring. All adults emerging from 84 cocoons attacked in the fall (Sep.-Oct.) underwent diapause and emerged the following spring. Thus, *Anastatus* displayed a "summer-autumn" emergence pattern similar to that of *G. apantelis* and *G. obscurus*, where early-season and mid-season progeny emergence was split between summer emergence, producing a summer gen-

eration, and autumn emergence to contribute to the production of the overwintering generation.

Muesebeck and Dohanian (1927) reported from New England that *A. pearsalli* (the major component of the *Anastatus* complex found in our Maryland study) develops in *C. melanoscelus* in 40 to 50 days. In their New England study, Muesebeck and Dohanian (1927) (usually) found only one generation a year for *A. pearsalli* (with 11 months or more spent in the host cocoon). This was clearly not the case in Maryland. The Maryland specimens that were clearly *Anastatus* n. sp. near *reduvii* generally emerged within 30 days of attack, while those that were clearly *A. pearsalli* usually emerged after at least 60 days in the cocoon, but at least one summer generation was observed for both species.

Arachnophaga picea attacks upon *C. melanoscelus* cocoons were recorded from mid-June through July at the Coastal Plains site, and from late-July through August at the Piedmont Plateau site. Cocoons attacked before early August led to adult hyperparasitoid emergence within 40 days of the attack. Attacks occurring from mid to late August resulted in diapause (spring emergence of adult hyperparasitoids).

Adult emergence of the Pteromalidae. *Dibrachys cavus* attacks upon *C. melanoscelus* cocoons in the Maryland study were recorded from May to October, with highest numbers of attacks recorded from June through September. Cocoons attacked before August led to direct adult hyperparasitoid emergence generally within 30 days of the attack (Table 3). Attacks occurring in August and September also resulted in part in direct emergence, but some diapause (spring emergence of adult hyperparasitoids) was noted. All progeny resulting from October attacks underwent diapause. Our results for Maryland were very similar to results in New England by Muesebeck and Dohanian (1927). They reported that *D. cavus* developed in 17 to 34 days, and could have up to 5 generations per year. They also noted that cocoons attacked prior to September 1 usually produced adults of the hyperparasitoid the same season, whereas those attacked after that date resulted in adult emergence the following spring (diapause).

Tritepitis scutellata was recorded only from the Appalachian Mountain site in our study. Attacks on *C. melanoscelus* were recorded only during July and August, with July attacks resulting mainly in direct adult hyperparasitoid emergence generally within 30 days of the attack, while August attacks led mainly to diapausing progeny.

Hypopteromalus inimicus was recorded from only the Piedmont Plateau site in our study, emerging from 7.1% of the parasitized cocoons at that site. Two broods were seen at the Piedmont Plateau site: one in May-June and the second in September-October. Cocoons attacked in May led to direct adult hyperparasitoid emergence generally within 30 days of the attack (Table 3). Nearly all the attacks occurring in September, and all those occurring in Octo-

Table 3. Emergence of indicated hyperparasitoids from *Cotesia melanoscelus* cocoons attacked during the indicated period of attack. Emergence can be direct (within 50 days), delayed (over 50 days but without overwintering) or in the spring after overwintering. Combined results for three Maryland locations for cohorts of cocoons exposed at two-three week intervals from March 1986 to March 1987.

Period of Attack	# Cocoons Attacked	Period of hyperparasitoid adult progeny emergence						Spring '87 (diapause)	
		May	June	July	Aug.	Sept.	Oct.	Nov.-Jan.	
<i>Anastatus</i> mixed species									
May	332	0	38	32	12	247	2	1	0
Early June	409		12	148	79	166	4	0	0
Late June	222			34	70	96	18	4	0
Early July	65			8	20	25	11	1	0
Mid-July	103			2	51	44	6	0	0
Late July	90				5	85	0	0	0
August	44					14	11	0	19
September	39								39
Oct.-Dec.	45								45
N	1349	0	50	224	237	677	52	6	103
<i>Dibrachys cavus</i>									
May	14	0	14	0	0	0	0	0	0
Early June	46		24	21	1	0	0	0	0
Late June	12			12	0	0	0	0	0
Early July	47			44	2	0	1	0	0
Mid-July	56				52	4	0	0	0
Late July	72				46	24	0	0	2
August	35				4	19	7	0	5
September	21						4		17
October	18								18
N	321	0	38	77	105	47	12	0	42
<i>Hypoteromalus inimicus</i>									
May	25	0	25	0	0	0	0	0	0
Early June	53		45	8	0	0	0	0	0
Late June	52			52	0	0	0	0	0
September	32						2	1	29
October	97								97
N	321	0	70	60	0	0	2	1	126
<i>Ooencyrtus kuvanae</i>									
March-May	58	19	37	2	0	0	0	0	0
Early June	2		2	0	0	0	0	0	0
Late June	15			15	0	0	0	0	0
Early July	7			7	0	0	0	0	0
Mid-July	12			1	11	0	0	0	0
Late July	77				71	6	0	0	0
August	298					86	212	0	0
September	8						5	3	0
N	477	19	39	25	82	92	217	3	0
<i>Eurytoma verticillata</i>									
Late July	7					1	0	0	6
August	71					5	0	0	66
September	41						3	2	36
N	119					6	3	2	108

ber result in diapause progeny emerging the following spring. Our insectary results for the first brood suggest that there is a summer generation for this species, but attacks from such a generation were not recorded in the field. The high levels of hyperparasitism recorded in the summer months (Wieber et al. 1995b) by other parasitoids may have obscured the summer generation of *H. inimicus* in this study. Therefore, we cannot say with confidence whether this species has two or three generations a year in Maryland.

Adult emergence of the Encyrtidae. *Ooencyrtus kuvanae* was active at all 3 Maryland locations from March through September. Adult progeny generally emerged in 30 to 60 days, but there was no sign of diapause even from September attacks (Table 3). However, little activity was noted for *O. kuvanae* during the winter. In his review of literature for *O. kuvanae*, Brown (1984) stated that no diapause had been reported for this species; however Weseloh (1986) subsequently demonstrated an effect of photoperiod on *O. kuvanae* progeny production. Cervara and Ham (1976) observed adults of *O. kuvanae* on gypsy moth egg masses during the winter, but there was no corresponding increase in parasitism prior to egg hatch. The trough in *O. kuvanae* attacks on *C. melanoscelus* during June-July (Table 3) may be caused by switching to freshly-laid eggs of *L. dispar*, which probably represent the preferred host. Two other species of encyrtids, *Ooencyrtus* sp. # 2 and *Cheiloneurus* sp., were incidental (7 and 2 specimens, respectively) hyperparasitoids in the Maryland study.

Adult emergence of the Eurytomidae. Muesebeck and Dohanian (1927) reported that in New England, *Eurytoma verticillata* (as *E. appendigaster* (Swederus), see Grissell (1985) for nomenclatural clarification) emerge in late May and early June, and attacks the first generation of *C. melanoscelus* cocoons. These produce adults the same season. However, a large proportion of these *E. verticillata* females live to attack the second generation of *C. melanoscelus* cocoons, joining the second (summer) generation to produce (mainly) diapausing progeny that carry the *Eurytoma* over the winter. Similarly, Weseloh (1978) found that individuals of *E. verticillata* were not reared from *C. melanoscelus* cocoons exposed before mid-June, 1975. By this time and after, incidence of diapause was high (about 90%). Attacks of *E. verticillata* occurred earlier in 1976, and while only 14.1% of cocoons exposed in late May that were so attacked underwent diapause, nearly 100% diapaused in cocoons exposed in July and after.

In our Maryland study, *E. verticillata* was recorded only from the Piedmont Plateau site, attacking 119 of the *C. melanoscelus* cocoons exposed at that site from late July through September. Only 11 of the *E. verticillata* adults emerged during the season of attack, with the remaining adults (108) emerging the following spring after undergoing diapause (Table 3). This is similar to the mid-summer situation reported in New England. While we recorded no attacks of *E. verticillata* in the spring or early summer in Maryland, we

assume that such early attacks would lead to a summer generation as reported from New England.

Perspective. The hyperparasitoid species monitored in our study have evolved several different strategies for apportioning their progeny to meet the challenges and opportunities of within-season (horizontal) and overwinter (vertical) propagation. The simplest strategy is that of *O. kuvanae*, which produces new broods all year long without any obvious need for diapause. Adults can be found attacking gypsy moth egg masses on warmish days throughout the winter. A more typical strategy used by *D. cavus*, *H. inimicus*, and *Gelis* species #4, is to produce a series of new broods until the late summer, and then to produce a brood that undergoes diapause with adult emergence in the spring. A more complex strategy is that used by *G. tenellus*, which, beginning in late spring, partitions its progeny so that some progeny emerge as an immediate summer generation, while others from the same attack cohort enter diapause and emerge in the spring. The percentage of each brood undergoing diapause increases as the summer progresses until by August, virtually all progeny undergo diapause. The most complex strategy is that of *G. apantelis* and *G. obscurus*, where, beginning in late spring, the progeny are partitioned so that some emerge as adults as an immediate summer generation, while others emerge in September to bolster the adult population that produces the diapausing generation. This pattern persists as the summer progresses, leading to a continuous emergence of multiple generations while simultaneously building up a fall generation upon which the overwintering survival of the species largely depends. Most of the individuals that diapause emerge from *C. melanoscelus* cocoons attacked in September or later. *Anastatus* mixed species display a similar strategy as *G. apantelis* and *G. obscurus*.

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